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## SEX RECOGNITION AND THE MATING BEHAVIOR OF THE WOOD FROG, *RANA SYLVATICA*.

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During the last three seasons while collecting amphibian eggs for use in some experimental work the writer had opportunity incidentally to observe some interesting behavior of the wood frog, *Rana sylvatica*. Inasmuch as the mating behavior and sex-recognition of this frog appear not to have been described in any detail it seems worth while to publish a digest of the rather extensive notes made during the times of observation.

Miss Hinckley<sup>1</sup> has reported some observations on the egg laying and incidentally refers to the activity and "quacks" or croaks of the males at the mating season. She gives some interesting temperature observations, stating that when the air temperature is 45° F. there is little activity of the frogs but that they float on the surface "like dead leaves," but that they spawn at 50° and that at 52° they are "active and clamorous." The mating season evidently begins earlier at Milton, Mass., where her observations were made, than at Cold Spring Harbor, for in 1880 she observed the frogs at ponds on Feb. 28 and in 1881 saw eggs and the quacking males on March 8.

Wright<sup>2</sup> describes the appearance of the eggs and gives the season at Ithaca, N. Y., as April 1 to 30.

The pond at which the writer mainly observed these frogs is perhaps 100 by 40 feet. It was formerly part of an artificial lake from which it was cut off by a grade intended for a railway. In the years since the grade has been abandoned the "Cut-off Pond" has become much filled up with leaves and other debris, so that now it is shallow, largely filled with leaves and much encroached upon about the margin.

<sup>1</sup> Mary H. Hinckley, "Notes on the Development of *Rana sylvatica* Leconte," *Proc. Bost. Soc. Nat. Hist.*, Vol. 22, pp. 85-95, 1882.

<sup>2</sup> Albert Hazen Wright, "The Anura of Ithaca, N. Y.: A Key to their Eggs," *Biol. Bull.*, Vol. 18, pp. 69-71, 1910.

The frogs were first observed in the breeding season in 1911 when on approaching the pond (March 30) at 100 yards' distance the writer heard a chorus of peculiar quawks. On nearing the pond the surface was seen to be constantly agitated and rippled in many places simultaneously by the movements of scores of frogs.

There have been 150 to 250 of these frogs at the Cut-off Pond each of the past three breeding seasons. The males lie on the surface of the water with outstretched legs each one quawking and swimming about at frequent intervals. The croak or short quawk differs decidedly from the croak of other frogs known to the writer. The note is not a distinct croak nor a peep but is a somewhat guttural, though not a coarse tone, perhaps slightly resembling the quack of a duck but more like the quawk of the night-heron. But it is a shorter note; it is not so loud and is less bird-like and more frog-like than the night-heron's call. The frogs have a single quawk or croak usually not repeated for some little interval. It is produced occasionally by the pairing males and frequently by the single males while lying quietly on the surface or resting partly upon a piece of brush or other debris. There is also a series of notes rather less loud and in slightly higher tone than the single call. This series is emitted by the males while swimming with a series of short, very rapid, leap-like strokes, a note accompanying each extension of the hind legs when the frog begins to swim. It is also sometimes made by a pairing male when with its mate it swims at the surface. Usually each successive note is less loud and each swimming movement less vigorous than the preceding one. The swimming movements of a series often continue after the calls cease. The series of calls, as well as the single note, when uttered by the pairing males is somewhat modified (apparently by the contact of the male's throat with the female's body) so that one can often distinguish the call of the pairing from that of the single male.

In swimming the head is held well out of the water and each stroke tends to push the frog more or less above the surface. The strokes are repeated in such quick succession that little advantage is obtained from the momentum acquired from the previous strokes and the tendency to push out of the water is

such that the progress made is relatively small. At the end of the series of swimming movements the hind legs are often vigorously extended alternately thus swaying or turning the body from side to side but resulting in very little forward movement. The series of short swimming movements are repeated by the individual at varying intervals from a few seconds to several minutes. When the activity is at its height few of the males remain inactive for as long as a half minute at a time and the calls from the numerous males make an interesting and peculiar and not unattractive chorus. The swimming movements are associated with seeking a mate. At the height of the chorus the frogs present a picture of remarkable activity for amphibians, the males swimming about and each attempting to mate with any frog or small moving object it encounters. Any individual which moves within a radius of several feet of another male is likely to be tested by him. The male thus approached sometimes swims away and sometimes actively resists but often pays no attention to the aggressor and the latter turns back, frequently without coming near enough to touch the male, and almost always the aggressor gives up the attack after the very beginning of an attempt to grasp the stranger with the fore legs. Often the one just attacked turns and "tries" the one that has just then given up an attack upon him but with an equally prompt cessation of the attempt. Seldom is an attempt made upon any but a moving individual. Even a female in the midst of a number of males may usually avoid pursuit as long as she remains quiet. On the other hand any small moving object at the surface of the water is most certain to be approached by an eager male. The writer twice observed a male approach a speckled tortoise when the latter thrust its head out of the water.<sup>1</sup>

The mating activities of the male frogs are not very readily interrupted. By moving quite slowly one may ordinarily approach to within a few feet of the active males without disturbing their chorus. When persons passed noisily by on the old grade however the chorus was more or less quieted, often stopped

<sup>1</sup> One suspects Miss Hinckley may have mistaken the mating activities of the males for she says (*l.c.*, p. 88): The "... presence of the females, who were largely outnumbered by the other sex, had evidently aroused a spirit of jealousy among them and each frog was intent on driving the others from the place."

entirely, and if the disturbance was considerable the males would leave the surface of the water. The renewal of the chorus was then uncertain. It might be renewed soon or not for an hour or two or if the air became cooler in the meantime it might not be heard again that day. The amount of disturbance required to interfere with their activities depended upon the degree of excitement of the chorus, and upon whether or not there had been any previous disturbance. Several times upon my approach to the pond during the breeding season a Cooper's or sharp-shinned hawk flew from a tree immediately over the pond. Few frogs were seen at the surface and these had only their heads protruding and many of them disappeared at the slightest unusual movement in the neighborhood. There seemed good reason to think that the hawk had been feeding upon the frogs, for it was seen there often and each time the frogs were less in evidence than otherwise noted during the breeding season when conditions were at all favorable for their seeking mates. At one time when the writer was at the pond a crow flew over casting a shadow across the pond and the chorus quickly died down and almost stopped but there being no further alarm it came up again at once. The following note was made after a hawk had been frightened away from the pond when the frogs had been much disturbed and the pond seemed almost destitute of frogs: "*Very few frogs visible. 15 minutes later one of the decoys in the bag croaked,—a submerged almost choked-off croak. It was followed soon by two or three other croaks from the same place and then one of those in the pond uttered a single croak and, the wave of confidence spreading, in two minutes the chorus was in full swing and the pond where all had been still as death was filled with active croaking tackling frogs.*" Such a speedy renewal of the chorus seems to indicate excellent perception on the part of the submerged males of the first sounds made by the few males at the surface.

The males remain at the surface at night when the air is not too cool and on one moonlight night the full chorus was observed at 10 P.M.

The behavior of the female wood frog is usually very different from that of the male. The female remains at the bottom of

the pond or clings to debris well beneath the surface and comes to the surface only occasionally. Even when unobserved by a male the female apparently does not remain at the surface for more than a few seconds at a time. When the female comes up she usually dodges under again at once to avoid the approach of one or more males. Sometimes she swims for a short distance on the surface and then goes under but more usually she dodges under at once and either remains beneath the surface or after swimming with a few long effective strokes comes up again some little distance away. The males follow a disturbance of the surface almost as readily as the moving object itself. If a female, though submerged, swims near enough the surface to produce some little ruffling of it, one or more males is very likely to follow the disturbance and attempt to seize the female when she comes up. Once in a while the female leaves the water and with long leaps moves about over the bank near the level of the water. She (as well as any male moving on the bank near the water's edge) may be pursued by males even here, though a capture on land was not observed.

The beginning of the attempt of a male upon a female is of course not in any way different from his approach toward another male but when he actually touches or often only nears the female his actions are usually very different for instead of the vigor and aggressiveness of the assailant rapidly falling off, as in case of one male approaching another, the aggressiveness is tremendously increased. The male makes every effort to catch the female if she is about to escape and often follows her under the water a little, but more often rapidly follows any disturbance of the surface and attempts to seize the female at once on her reappearance. If a male once succeeds in clutching with the fore legs any portion of the body of a female he cannot be dislodged, though the female continues to struggle. The male quickly brings himself to the pairing position, sitting upon the female's back. The fore legs are tightly clamped about the female with the first toes extended and deeply depressed against the ventral body wall of the female just back of the pectoral girdle. Often two or more males pursue a female at the same time and in case one male gets a hold on the dorsal side of the female and anterior to a second male the latter

is most certain to be dislodged by the vigorous kicks of the other. If however a second male, as rarely happens, succeeds in getting well beneath the first so as not to be readily reached with the latter's hind legs the first male is very likely to be pushed upward and away from the female's body except for the clasping fore legs. In such a case he soon releases his hold. Amid the great preponderance of males the most vigorous and active ones are more likely to secure mates and to keep possession of them and effect fertilization of the eggs.

The female when in copulo does not so generally remain beneath the water as when unpaired, though much the greater part of the time is still spent upon the bottom or on submerged brush. It is possible of course that when a certain physiological state supervenes the female remains more at the surface than previously and this subjects her to the attacks of the males so that she does not long escape a mate, and that the pairing female does not remain more at the surface than she would if no male found her. It is certain that whereas the unpaired females are not rarely seen momentarily at the surface they very rarely remain for even a few seconds. The female is generally considerably larger than the male and is able to swim about readily with the smaller male upon the back. The male sometimes aids in swimming but usually remains passive regardless of the movements of the female. When approached by another male however the pairing male makes a vigorous defence with the hind legs and this with the struggles of the female usually serves to dislodge the intruder. But the struggles of the female and the resistance of the male are not always successful in warding off a second male. In the height of the pairing season there is usually to be seen one or more cases of more than one male clasping hold of a female. Such a multiple copulation is fraught with danger to the female as well as to the more successful males. There is a constantly recurring struggle on the part of the rival males for possession of the female. Unless the female is able to leave and remain beneath the surface these struggles are certain to attract other males which also attempt to get possession of the female. The result is a struggling, writhing mass of males holding on to the female and to the males already

clasping the female. Each male strives to get into a more favorable position and (incidentally) to push off the other males. In one mass the female was lying on one side with the head under water and was apparently dead, while five males were holding to her and to one another in various positions and several other males were making occasional efforts to fasten hold on the bunch. Another such mass was lifted out in a dip net and when separated was found to consist of six males and the female. Five other males had been attempting to take part in the struggle but were not holding fast to the mass, avoided the net, and escaped. Sometimes the pairing female leaves the water but since she does not stray far from the water's edge she is frequently followed by one or more males.

Copulation may continue for a day or two. Pairs were kept in the laboratory together for thirty-six hours or longer. The embrace is so strong that in forcibly dislodging the male one fears lest the force employed must break the animal's leg. One male was found clasping a small male green frog and another late in the breeding season was found clutching a dead and somewhat decomposed female wood frog.

The wood frog first appears at the ponds in spring after a general thaw and several successive warm days. So far as observed at the Cut-off Pond the mating season was from March 30 to April 4 in 1911; March 28 to April 5 in 1912; and March 15 to 24 in 1913. It is possible that these do not represent the extreme dates for the end of the season. In one other pond near Cold Spring Harbor these frogs sometimes begin mating a day or two before they do in the Cut-off Pond and in a third pond wood frogs do not appear for several days after the first eggs are laid in the Cut-off Pond. Similar and much larger differences in times of egg-laying, in these three ponds, are observed with *Ambystoma punctatum*. These are presumably due entirely to temperature differences at the different ponds. One of these ponds is in a more sunny situation than the Cut-off Pond and the other is on a north slope.

The males apparently reach the pond first. In 1912 the chorus was in full activity March 28. The pond contained little water and there were perhaps 250 males in an area some 50 by 16 feet.

But no females were in evidence while on the following day they were as abundant as they ever appear. The females are much less numerous than the males. One is convinced that there are at least a dozen and possibly twenty males to every female. It would be easy to overlook the females entirely except during the height of the pairing season when by careful observation one can usually locate a few pairs, though the writer has never been able to find as many as a dozen pairs at a time in the whole pond, including those at the surface and the ones visible under water. The arrival at the pond was observed in the case of two females (forenoon of March 29, 1912). The behavior of one of these was noted as follows:

"Saw a female, a very light reddish orange one, enter the pond from the up-hill side. Saw her distinctly as she left the bank, made four or five bounds before reaching the water and plunged in without hesitation. Swam under at once and went for a distance of ten feet under the water, then came up again but dodged under when a male approached and went under a submerged leaf. She came to the surface again in seven minutes, then went under a leaf again and in the next five minutes repeated these movements two or three times. All the time she was getting farther away from the center of the chorus where she had entered the pond. Later she swam along the edge under water and away from the chorus and came to the surface twice, then swam across the pond under water and did not come up at once. Her actions could not be followed longer."

From such observations it seems evident that the females (and doubtless the later arrivals among the males) are attracted to the pond by the croaking males but that once in the pond the females endeavor to avoid the males, at least for a time.

The frogs generally remain at the pond only as long as the mating activities last. The females are apparently much weakened by the mating and egg-laying activities. Spent females were observed leaving the pond while the chorusing of the males was still at its height. Such females appear to be as attractive to the males as before laying the eggs and attempts to leave the pond are often frustrated by the active males.

The departure of males was less often observed and appears to

occur in general only when the egg-laying is nearing completion, though a few males were seen well up the bank and apparently leaving the pond soon after the chorus had passed the climax of its activity. The sperm ducts of some of these were examined to see if perchance they might appear to be males which had discharged their sexual products, but no consistent difference was noted between those males leaving and the actively chorusing males still on the pond.

Most of the egg-laying, if the weather continues mild, occurs within two days. The eggs are laid in enormous aggregations, the bunches from the different females being crowded closely together. In 1912 all the eggs in the Cut-off Pond were laid within a radius of three or four feet. In 1911, and again in 1913, there were two such aggregations in the pond.

The indiscriminate trying by the males of every individual encountered aroused the writer's interest in the mode of sex-recognition. In an attempt to find the basis for sex-recognition a number of experiments were tried, in each of which a frog was fastened upon a light fishing line by hooking through the jaw and used as a decoy among the chorusing males at the pond. A long pole was used to hold and manipulate the decoy. The live frogs so used, unless tired out, swam about and acted apparently in a normal fashion, though the active females could not be kept at the surface without considerable manipulation.

The following notes were made on the spot, most of them March 30, 1912, and illustrate characteristic behavior of the mating frogs.

*Experiment 1.*—A male which had been pairing with a female in the laboratory all night was forcibly separated from its mate and tried on the line but with no further result than to be approached or tackled by practically every male which happened near him.

*Experiment 2.*—Placed a male paralyzed in the hind legs on the line and kept it moving somewhat. While tackled many times it was quickly released and in fact more often was merely quickly approached and not actually touched. One male however took hold and clasped him for several seconds, perhaps forty, but released him readily when I tried to simulate movement of a female by moving the line to which it was attached.

*Experiment 5.*—11 A.M., captured a female which had already deposited the eggs and was leaving the pond. This was used as a decoy and while one male approached somewhat and failed to grasp her the second and third made desperate efforts to get her and the latter succeeded in spite of her diving. The male dived after her but seemed unable to follow her well under water and caught her when she came near the surface and was soon in normal position.

*Experiment 8.*—Separated a pair and placed the female (still with eggs) on the line. She was soon captured, though she appeared to make every effort to dodge and escape the males.

*Experiment 9.*—A female, a large reddish brown one, was removed from a pair and placed on the line. There was seldom a male lost opportunity to grasp her and two or three would pursue her at once and fight vigorously for possession. Often I pulled her out of the water with a male ventrad and one dorsad though the former always let go before being swung in. Caught as many males as I wished by simply allowing them to grasp her and then swinging her in shore. Hauled in five in this way in less than three minutes and nearly all that time was spent in freeing the female for she was grasped as soon as brought near a male whether she was dorsal or ventral side up, at the surface or almost submerged. An hour later she was killed (pithed) and males seized her apparently quite as quickly and vigorously and struggled quite as hard for possession as before. Later when stripped of her eggs she was seized almost, though I think not quite, as readily as before. But it was getting late in the day and the air was becoming considerably cooler.

*Experiment 10.*—A dark female captured while leaving the pond on the up-hill side was used as a decoy. This one was so like a male in color, size and general appearances that it was only by examining the first fore toes and opening her that I could be positive of her sex, though I suspected it by the behavior of the males. It would seem that the frogs could scarcely recognize her as a female by sight. While she was not tackled as often or as vigorously as the reddish brown female (Exp. 9) yet during the hour she was observed she was paired with by five different males, none of which released her except when forcibly removed.

*Experiment 14.*—A dark female, *with eggs*, was paired with readily though my impression was that it was not so eagerly pursued and seized as the reddish brown ones.

*Experiment 19.*—Thinking a chemical sense perhaps involved in sex-recognition, tried a male with the contents of the cloaca and uterus of a female smeared over the posterior portion of his body. There were no more reactions than common to a male though I tried several times and with the cloacal parts of two females, one of which was the reddish brown one (Exp. 9) which had seemed particularly attractive to the males and with which so many males had been captured. The male probably did not retain the material on his body long when moved in the water. Several times however the decoy was gotten near a male before there had been much chance for the material to become washed off.

From these and other experiments it was made clear that the females alive or dead with or without eggs were recognized by the males though the dark ones without eggs were not so eagerly seized as the reddish brown ones and the dark ones still with the eggs were probably less readily recognized than the brown ones.

As regards sex-recognition the behavior of these frogs may be stated as follows. The males test every frog or moving object within a radius of several feet. As compared with the male the different behavior of the female in the pond probably serves as a partial means of sex-recognition. One gains the impression that he can distinguish a female in the pond as far as she is readily visible, for the female swims with long gliding strokes mostly under water, usually comes to the surface only momentarily and dodges under on the approach of another frog; while the males swim at the surface, swim about with short ineffective strokes and commonly make little effort to avoid an approaching frog. On the other hand occasionally a female swims at the surface with movements apparently indistinguishable from those of a male and on at least two occasions such females were pursued with remarkable persistence by one or more males. It is to be noted in this connection also that a rapidly swimming or persistently swimming male or the struggles of more than one

male over a female attract males from all directions. Hence sex-recognition on the basis of method of movement can be only very tentative and preliminary.

The female wood frog when attacked by a male apparently makes every effort to escape both on the approach of the male and when he attempts to gain a hold on her. After the hold is once gained her struggles cease. When the male is approached by another male he sometimes apparently resists as vigorously or perhaps even with greater effect than the female, for she is heavy with eggs. But more often the male makes little or no show of resistance and is apparently as quickly left alone whether he resists or not. Hence there seems no consistent difference in the resistance offered by the two sexes when seized by a male.

The females at the breeding season, at least before the eggs are laid, are nearly all in the reddish brown color condition while the males are much darker. But exceptions to this color distinction between the sexes have already been noted. It is possible however that the color of the female plays some part in sex-recognition, for when used as decoys the dark females which had deposited the eggs were less frequently paired with than the reddish brown ones and this was possibly true to some extent with a dark female which still retained the eggs.

Thus it appears that the color of the female may *possibly* be a factor and that the peculiar behavior of the female is *probably* a factor in sex-recognition. But there seems unquestionably another factor involved when the male approaches closely or touches his prospective mate. Males were seen time and again to approach eagerly to within a few inches of other males only to turn back without coming into contact with or actually attempting to seize them. To be sure two or three instances of such behavior were noted when a male approached a female but they were most exceptional. When a male approaches nearly to a female his activity increases tremendously, in many cases before he can have actually touched her. On one occasion a male was seen to stop swimming within eight or ten inches of an unpaired female which was resting quietly at the surface. After a short time, perhaps ten or twenty seconds, with a rapid and vigorous movement he suddenly seized the female. The suddenness and

rapidity of the movements suggested to the observer that possibly sex-recognition may have become complete at this distance before the male moved. No similarly vigorous attack upon a quiet male was observed though at times part of the pond contained a male frog for almost every square foot of surface.

Dead females are distinguished from dead males.

The readiness with which the attempt of a male to pair with another male is given up on near approach, the keenness of the male's pursuit after once approaching very near or touching a female, and the discrimination between a dead male and a dead female particularly in cases in which, to the human eye, the latter is indistinguishable in size, color and general features from a male, suggest that a chemical sense is involved in final sex-recognition though one experiment designed to test this hypothesis was unsuccessful.

The writer regrets his inability to further pursue the subject experimentally, but the pressure of other work left no opportunity to work on the problem during the height of the breeding season in 1913 and such will probably be the case in future seasons.